Nest aggregations of wild bees and apoid wasps in urban pavements: a “street life” to be promoted in urban planning

Grégoire Noël[1$], Violette Van Keymeulen[1$], Yvan Barbier[2], Sylvie Smets[3], Olivier Van Damme[3], Gilles Colinet[4], Sophie Lokatis[5], Julien Ruelle[6] & Frédéric Francis[1]

[1] Functional and Evolutionary Entomology, Gembloux Agro-Bio Tech, University of Liège, Passage des Déportés 2, 5030 Gembloux, Belgium

[2] Service public de Wallonie, Département du Milieu Naturel et Agricole, Avenue de la Faculté, 22, B-5030 Gembloux, Belgium

[3] Belgian Road Research Centre (BRRC), Boulevard de la Woluwe, 42, B-1200 Woluwé-Saint-Lambert, Belgium

[4] Soil-Water-Plant Exchanges, Gembloux Agro-Bio Tech, University of Liège, Passage des Déportés 2, 5030 Gembloux, Belgium

[5] Institute of Biology, Freie Universität Berlin, Berlin, Germany

[6] Département Développement Nature et Agriculture – Bruxelles Environnement (BE), Site de Tour & Taxis, Avenue du Port 86C / 3000, 1000 Bruxelles, Belgium

[$] These authors contributed equally as first co-author

Corresponding author: Grégoire Noël (gregoire.noel@uliege.be)

Available ORCID numbers :

- Grégoire Noël: 0000-0001-5994-1022
- Yvan Barbier: 0000-0002-4380-0505
- Gilles Colinet: 0000-0002-1850-5504
- Frédéric Francis: 0000-0001-7731-0849
- Sophie Lokatis: 0000-0003-2178-3924

Abstract

In the last 10 years, knowledge of wild bees and apoid wasps' community dynamics has gained interest in urban ecology focusing on the availability of floral resources in cities. Although unstudied, the urban environment impacts the conditions of their nesting sites. Recent observations in the Brussels-Capital Region (Belgium) showed that urban pavements can be an alternativenesting opportunity for ground-nesting Hymenoptera such as wild bees and apoid wasps. Here, using citizen science, we investigated the richness of ground-nesting species living under urban pavements, the preferences of the sidewalk type and joint size. We assessed the impact of soil texture under the pavements on the nesting site selection for each ground-nesting species. A total of 22 species belonging to 10 families of wild bees and digger wasps with their associated kleptoparasites were identified around 89 sites in the Brussels-Capital Region. Sandstone setts or concrete slabs with an unbound joint size around 1 cm were found to be the best suitable urban pavements for the ground-nesting species. The soil texture under the pavement was mainly sandy among our samples. Finally, we also suggest engineering management guidelines to support bee and wasp species nesting under urban pavement in highly urbanized areas. Such observations pave the way for further research in the field of urban ecology to develop multifunctional pavement designs that promote biodiversity.

Keywords: Anthophila, Apoidea, nesting behaviour, urban ecology, urban ecosystem, urban conservation

Introduction

Rapid urbanization is one of the most critical drivers of global biodiversity loss (Ives et al. 2016; Pauleit et al. 2016) (Wastian et al., 2016). Recognizing the role that cities play in tackling the global biodiversity crisis, preserving and fostering local biodiversity has become a key objective for municipalities around the world (Pierce et al. 2020). The goal of urban nature strategies, generally, is not only to protect and preserve biodiversity, but also to enhance ecosystem functions, and to grant a now predominantly urban population access to nature in their day-to-day life. Urban nature however sometimes sprouts in unexpected places, and urban dwellers, and ecologists alike, have not payed much attention to the ecosystem that is spreading in the cracks and joints of urban pavements. Urban pavements provide alternative nesting opportunities for certain ground-nesting species, but although the sandy mounds that generally indicate their presence are known to be quite present in several European cities (pers. comm. Volker Haeseler and Christian Schmid-Egger), only few studies have addressed urban pavements as habitats for aculeate insects (notably Haeseler 1982; Pauly 2019a).

Hymenopteran communities are sensitive to urban landscape conversion (Buczkowski and Richmond 2012; Geslin et al. 2016; Corcos et al. 2019; Theodorou et al. 2020a): flower resources are becoming scarce under the pressure of urban fragmentation, and urban soil is rendered impervious by concrete, asphalt and other pavement, which makes the ground uninhabitable to ground-nesting hymenopterans (Burkman and Gardiner 2014; Harrison and Winfree 2015; New 2015; Geslin et al. 2016; Wenzel et al. 2020a; Ayers and Rehan 2021). Research has shown a decline in richness and size of urban bee communities as urbanisation increases (Ahrné et al. 2009; Fortel et al. 2014; Eggenberger et al. 2019), and the decline of predatory species like wasps (Abrahamczyk et al. 2020). These are additionally affected in their ability to locate prey in large landscape, which is disrupted by the habitat fragmentation caused by the urban matrix (Kareiva 1987), leading to changes in the community structure of apoid wasps in cities (Christie and Hochuli 2009; Burkman and Gardiner 2014). Paradoxically, recent studies have shown that cities can also serve as refuges for wild bee communities (Baldock et al. 2015; Hall et al. 2017; Theodorou et al. 2020b). In urban areas, several factors can be potentially beneficial to hymenopteran communities, and wild bees in particular: (i) the amount and coverage of biocidal particles in cities tends to be lower than in the surrounding countryside, (ii) the urban heat island phenomenon favours the presence of thermophilic species, (iii) the heterogeneity of urban patches offers a wide diversity of habitats with multiple associated ecological niches and (iv) urban parks, gardens and other green spaces generally provide sufficient floral resources distributed throughout the year (Fortel et al. 2016; Wenzel et al. 2020b; Fenoglio et al. 2021). A surprisingly large number of cavity-nesting species might even benefit from artificial nesting aids (MacIvor 2017), but the more than half of the 403 species of Belgian wild bees are nesting in the ground (Drossart et al. 2019).

Solitary bees build their nests underground. These typically consists of an entrance, surrounded by soil tumulus (Fig. 1a), which extends into a main gallery branched into secondary galleries containing the larval cells that contain food resources (a mixture of pollen and nectar) and one or multiple eggs each (Malyshev 1935; Michener 2007). Ground nesting behaviour is typical for Andrenidae and Melittidae families as well as the majority of Halictidae and Colletidae families (Danforth et al. 2019). Apoid wasps - including families that have recently been up-ranked (e.g., Philantidae, Psenidae, Bembicidae, Pemphredonidae) by Sann et al., (2018) - also play important ecological roles in urban environments. Adults behave as flower visitors, and as predators they capture insect or spider prey to feed their offspring (Bitsch and Leclercq 1993). In Belgium, 199 species of apoid wasps have been documented with more than a half of them nesting in the ground (i.e., 107 spp.) (Pauly 1999; Rasmont and Haubruge 2002). Some aculeate species may exhibit a collective nesting strategy in nest aggregation such as *Cerceris* spp. (Willmer 1985; Polidori et al. 2006) or *Andrena* spp. (e.g. in Fellendorf et al. 2004). In ground-nesting wild bees, sub-social and semi-social behavior is distributed especially among some *Lasioglossum* species such as *Lasioglossum laticeps* (Schenck, 1869) (Packer 1983).

Bee and wasp species that nest in the ground can potentially also inhabit urban pavements, if the conditions are met. Joint size might have a direct effect on the nesting ability of the bees and wasps: if the joint size is smaller than their thorax size, they will not be able to dig a gallery. The soil texture (Cane 1991) , the soil cover (Nichols et al. 2020), the soil compaction (Wuellner 1999; Sardiñas and Kremen 2014), the soil humidity (Wuellner 1999), the soil temperature and its sun exposition (Potts and Willmer 1997), and the soil aspect (Cane 2015) can influence the selection of the nesting site. In Brussel-Capital Region (BCR), the pavements are builded according to the jointing material. Only the modular pavements (i.e., the slabs are separated by jointing material) are supposed to host Hymenoptera nests. To reach the soil below the pavement plates, digging insects will have to enter through the joint. The nature of the jointing material thus defines the hardness of the substrate and therefore influences the ability of bees and wasps to tunnel into it, acting as a filter in nest site selection. Also write something very brief about pavement types – it is very unclear what is meant.

As a pioneering study in the urban ecology of ground-nesting Hymenoptera, we addressed the following questions about the community of wild bees and apoid wasps according to their nesting preferences in pavements: (i) what species inhabit the pavements in the Brussels-Capital Region (BCR)? (ii) Is there a relationship between the size of ground nesting species and the size of the joints? (iii) Does the pavements type have impacts species composition? (iv) Which soil texture under the pavement is favoured by ground-nesting species? To address these questions, we asked volunteers/engaged volunteers in data collection and asked citizens to look for nesting sites throughout the city of Brussels. In a second step, the preidentified sites were visited and sampled by experts. Finally, we characterized the edaphic features of the species identified. The implications of our results are discussed in relation to the current challenges of designing urban pavements to encourage ground-nesting insects and human-wildlife cohabitation in cities.

Material and methods

Identification and validation of the potential study sites

As part of a general assessment of wild bee communities in the Brussels-Capital Region (BCR), Pauly (2019a) reported 4 nesting sites in urban pavements. In order to gain more knowledge about this highly understudied habitat, we applied a crowdsourcing method based on citizen science (Newman et al. 2017). We first created and actively disseminated a participatory survey to BCR citizens on social networks in collaboration with the communication department of Brussels Environment and other key actors in BCR conservation (e.g., regional and local institutions). The online form was launched on March 11, 2020 before the first emergence of the potential hymenopteran insects (Pauly 2019a). The participatory survey ended on 17 July 2020. Participants were asked to enter information on (i) the BCR municipality, (ii) the street name and building number, (iii) the date of the last observation, (iv) an image of the nest or the insect (facultative). We removed observations (n = 74) unrelated to taxa and location of our study sampling strategy :ant nests (Fig. 1b), cavity-nesting bees, and locations outside of BCR. A total of 89 locations were found suitable for further field observation and visited within 1-7 days after transmittal. On site we examined the pavement cover for 30-45 min. Field work was performed on sunny days with clear sky, little wind (less than 15 km/h) and a daily minimum temperature of 15°C between 09:00 and 17:00 (Ahrné et al. 2009; Fortel et al. 2014). A site was validated if: (i) a bee or wasp showed evidence of entry or exit into a nest between the paving slabs and/or (ii) a cuckoo species (i.e., cuckoo bee or wasp) patrolled near a sandy mound on the pavement..

Data collection on validated sites

The number of nests was estimated by counting the sandy mounds. On each of the selected sites, each morphologically distinct specimen was captured and killed *in situ* with ethyl acetate ($C_4H_8O_2$) for later species identification. Joint size was measured on 6 nests randomly selected within a site using a millimetre bar near the nest entrance . If more than one ground-nesting species was present at a site, measurements were taken randomly across the site without distinguishing between species. The joint structure variable was added to the database as a nominal qualitative variable with 2 modalities: degraded rigid joint (Fig. 1c) or unbound joint (Fig. 1d). The type of pavement was assessed from photographs and classified according to 3 modalities: concrete slabs (Fig. 1c); sandstone setts (Fig. 1d) and other types, including ceramic slabs, concrete pavement, limestone (Belgian blue stone) and porphyry setts. Finally, the position of the nest on the pavement was recorded as a qualitative variable according to the following nomenclature: pavement; front of house; internal yard; road with car traffic or other (embankment, junction by pavement and embankment or junction by internal yard and pavement) The sand of the mounds was collected randomly from 3-10 nest entrances (max. 50g) on pavements as corresponding to the soil layer excavated by the digging activity of insects under the pavements (Fig. 1a). Based on preliminary results of the substrate texture under pavements, sandy mounds seem to be a good proxy of soil texture (see in supplementary information S1).

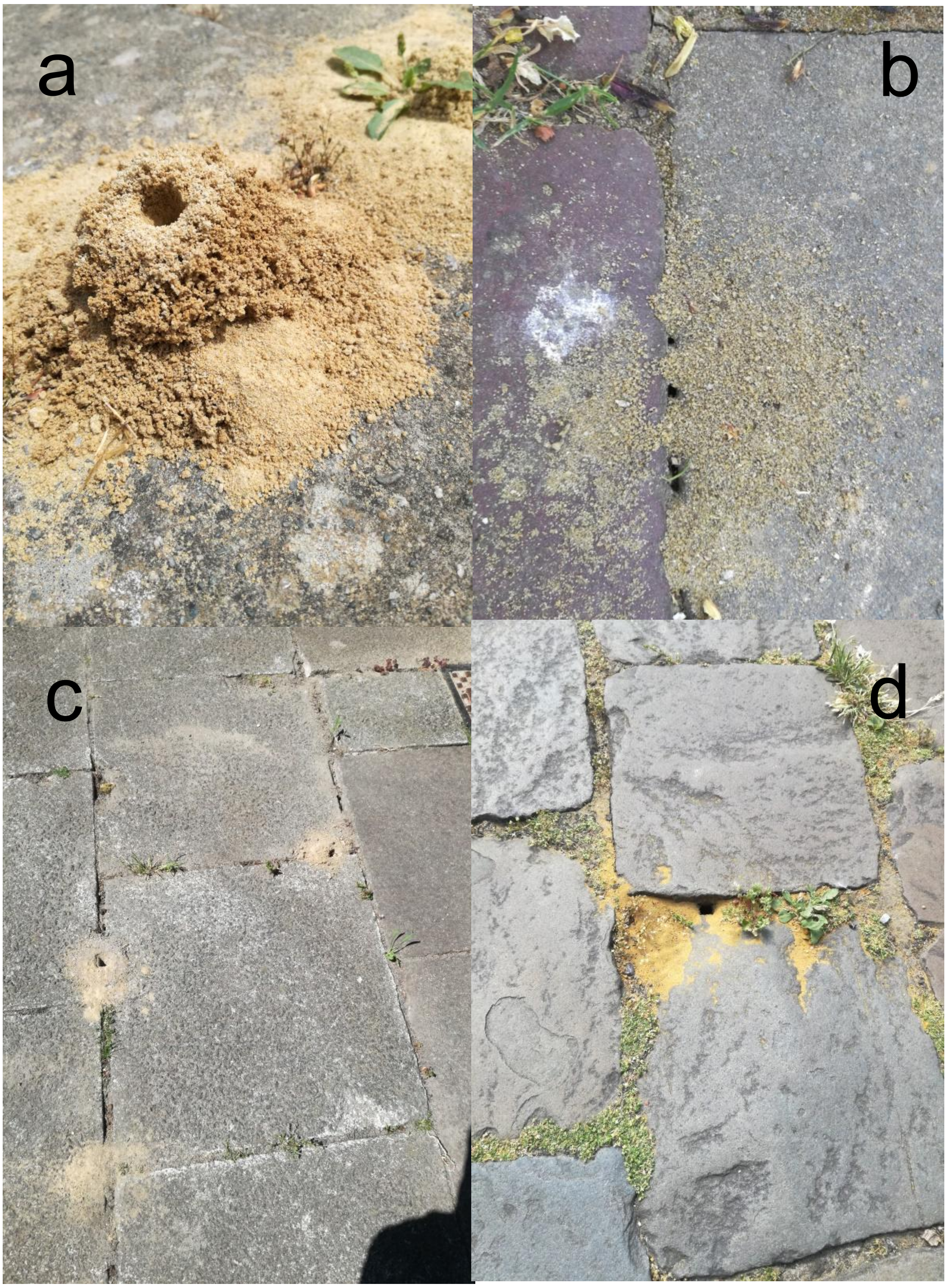

Fig. 1 Nest pictures on pavements. Sandy mound (Auderghem, Brussels) (**a**). Ant nest (Anderlecht, Brussels) (**b**). Degraded rigid joints of concrete slabs (Schaerbeek, Brussels) (**c**). Unbound joints of sandstone setts (Schaerbeek, Brussels) (**d**). Pictures by Grégoire Noël.

Laboratory data collection

All collected specimens were prepared for identification following Mouret *et al.*, (2007). Several identification keys were used to identify bee and wasp species (Bitsch and Leclercq 1993; Bitsch et al. 1997, 2007; Falk 2015; Pauly 2019b). All identified bee specimens were checked against the reference collections of the Functional and Evolutionary Entomology Laboratory (ULiège), the collections of Alain Pauly for captured Halictidae species and the collections of Jean Leclercq for apoid wasp species.

Sand mound samples were weighed using a precision balance and passed through a sieve shaker (Haver & Boecker VWR brand) for 10 minutes at an amplitude of 1 mm through five sieves with mesh sizes of 1 mm, 500 µm, 200 µm, 100 µm and 50 µm in order to distinguish sands from clays and silts (50 µm threshold) and to differentiate between very fine, fine, medium and coarse sands. The particles retained by each sieve were then weighed and their value converted to a percentage of the total sample volume. This conversion eliminates weight variations due to sample moisture and provides a common basis for comparison between samples of different weights. Although the particle rate of silts and clays was not distinguished, we can approximate the average and extreme textures of the collected mounds using the texture triangle by halving the remaining percentages between the silt and clay classes.

Mapping and statistical analysis

All analysis were performed in the R software environment (R Core Team 2020). Validated sites were mapped using the *mapview* R package (Appelhans et al. 2019). The average mean joint size per site was then assigned to the corresponding species. For the joint size, we used an ANOVA after descriptive statistical analysis of the data to compare joint size measurements between selected ground-nesting species and between their respective families. For statistical analysis, we excluded cuckoo species due to their nesting strategy and the specimens from the families Bembicidae, Crabronidae, Psenidae and Pemphredonidae because we did not record their respective joint sizes (see Table 1). A *post-hoc* Tukey test with adjustment for multiple comparisons was applied to compare the pair mean of joint size. We also measured the inter-tegular distance (ITD) – the distance between the two wing insertions - of female individuals only, which is a proxy for their size (Kendall et al. 2019) using a digital caliper (Electronic Digital Caliper). We evenly distributed the ITD and joint size measurements by species present at the site. A Gaussian linear regression was performed to test the relationship between species size and average mean joint size.

For the particle size analysis, a principal component analysis (PCA) was performed to determine whether similarities in particle size preferences among ground-nesting species could be attributed to specific families (as shown in Table 1) using *factoextra* (Kassambara and Fabian 2020) and *FactoMineR* (Lê et al. 2008) R packages. Graphs were plotted using the *ggplot2* R package (Wickham 2016).

Results

Participatory survey and site validation

Between 5 April and 31 July 2020, 163 sites throughout BCR fulfilled the criteria for our online form and were surveyed subsequently. A total of 89 sites have been? validated (Fig. 2). The municipalities of Ixelles (n=16), Watermael-Boitsfort (n=13) and Uccle (n=13) had the largest number of sites, while only few sites were situated in Berchem-Saint-Agathe (n=1), Forest (n=1) and Auderghem (n=2) (Fig. S1). There was no coding by citizens of Saint-Josse ten-Noode and Koekelberg municipalities.

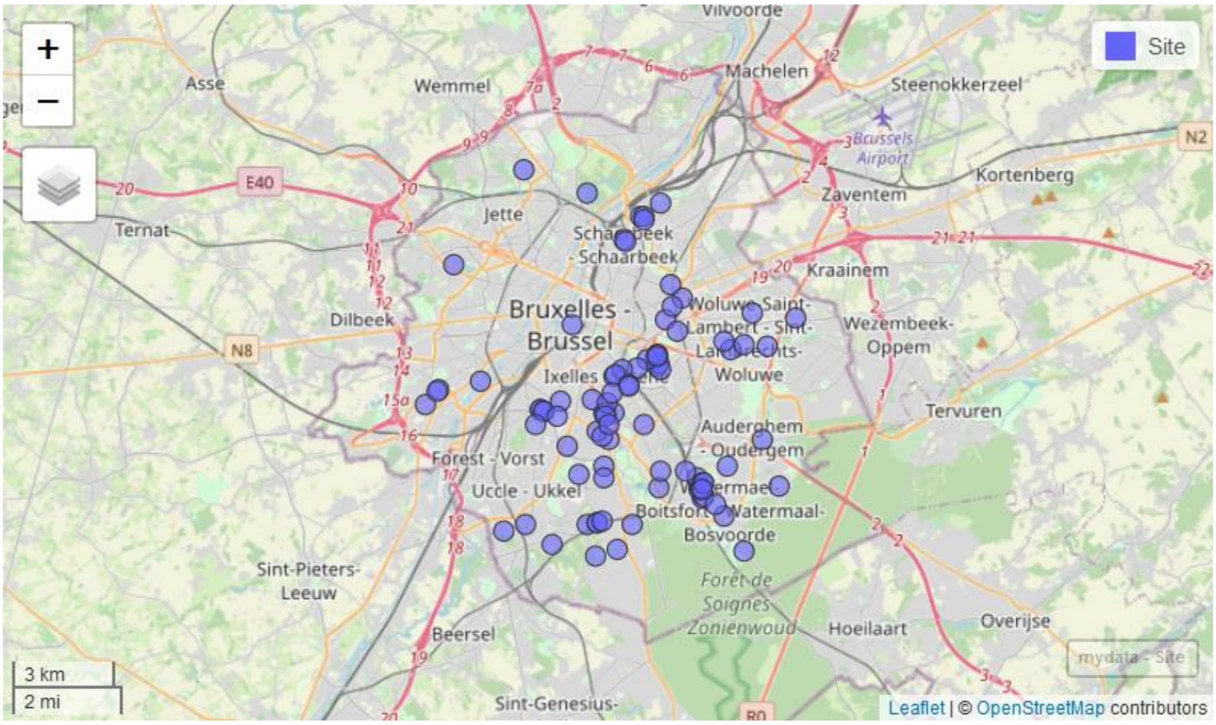

Fig. 2 Distribution map of the validated study sites in Brussels Capital Region (N=89)

Species recorded

We collected 153 specimens belonging to 22 species including 11 solitary bee species, 9 apoid wasp species and 2 chrysid species (Table 1).

Table 1 List of apoid and chrysid families (in bold) and species collected at all sampling sites. The specific abundance is presented on the right side of each species. Species names in black correspond to ground-nesting, non-parasitoid species, while cuckoo species are highlighted in red. The apoid wasp families were defined according to Sann et al. (2018).

Solitary bees	Total/number	**Apoid and chrysid wasps**	Total/number
Andrenidae	**33**	**Philantidae**	**37**
Andrena barbilabris (Kirby, 1802)	*30*	*Cerceris arenaria* (L.)	*26*
Andrena vaga (Panzer, 1799)	*3*	*Cerceris quadricincta* (Panzer, 1799)	*4*
Melittidae	*8*	*Cerceris rybyensis* (L., 1791)	*5*
Dasypoda hirtipes (Fabricius, 1793)	*8*	*Philanthus triangulum* (Fabricius, 1775)	*2*
Halictidae	**36**	**Bembicidae**	**1**
Lasioglossum fulvicorne (Kirby, 1802)	*2*	*Gorytes planifrons* (Wesmael, 1852)	*1*
Lasioglossum laticeps (Schenck, 1868)	*20*	**Crabronidae**	**6**
Lasioglossum sexstrigatum (Schenck, 1868)	*7*	*Lindenius pygmaeus armatus* (Rossi, 1794)	*4*
Sphecodes crassus Thomson, 1870	*2*	*Oxybelus bipunctatus* Olivier, 1812	*2*
Sphecodes miniatus Hagens, 1892	*1*	**Psenidae**	**2**
Sphecodes monilicornis (Kirby, 1802)	*1*	*Mimesa lutaria* (Fabricius, 1787)	*2*
Sphecodes pellucidus Smith, 1845	*3*	**Pemphredonidae**	**3**
Apidae	**5**	*Diodontus insidiosus* Spooner, 1938	*3*
Nomada alboguttata (Herrich-Schäffer, 1839)	*5*	**Chrysididae**	**22**
		Hedychrum gerstaeckeri Chévrier, 1869	*4*
		Hedychrum nobile (Scopoli, 1763)	*18*

The most abundant species found at the study sites were *A. barbilabris*, *C. arenaria*, *L. laticeps* and *H. nobile*. We also collected corresponding cleptoparasite and parasitoid species, namely *N. alboguttata*, *Sphecodes* spp., *H. gerstaeckeri*, and *H. nobile* (Table 1). Most sites had a single ground-nesting species (excluding cleptoparasite and parasitoid species). However, some of the sampled sites showed that co-occurrence of several nesting species was possible between solitary wasps and solitary bees, but also between different bee species and between different wasp species (Fig. S2).

Joint Size Analysis

A total of 398 joint measurements at 69 validated sites corresponded to the nest entrance locations of 10 ground-nesting species (Fig. 3). The mean joint size for all species was 1.08 cm ± 0.57 cm with a maximum measured at 3.00 cm and a minimum at 0.20 cm. Details for all studied species are given in Table S1. A significant difference in mean joint size was observed between different ground-nesting species (F-stat = 1.97; df = 9; p-value = 0.041). However, after adjusting for multiple comparisons, no pairs of species differing in their joint size were detected (p-value > 0.05). After excluding 9 sites due to degraded individuals (without ITD measurements), the linear regression of the mean joint size and ITD size was performed on 80 observations of ground-nesting specimens. ITD did not explain the selection of joint size among the species (F-stat = 0.16; df = 78; p-value = 0.69; Fig. 4).

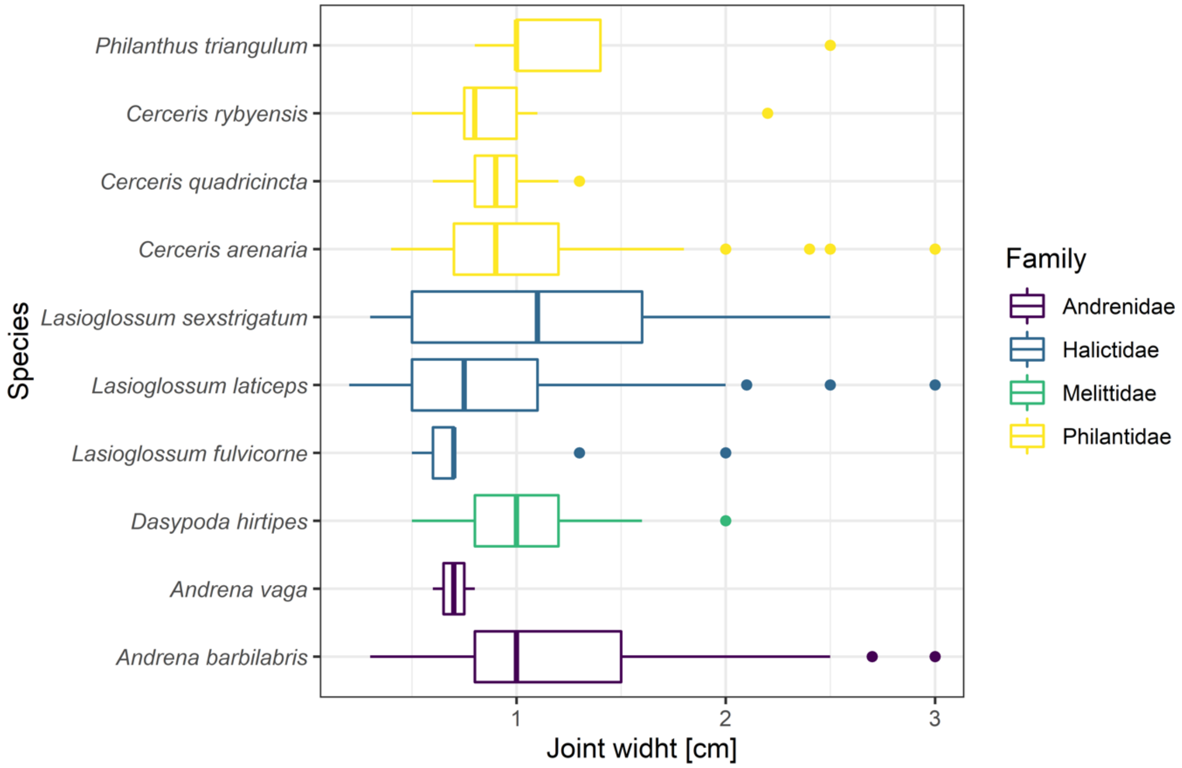

Fig. 3 Distribution of joint sizes for nest entrances (in cm) according to different ground-nesting species and their respective families.

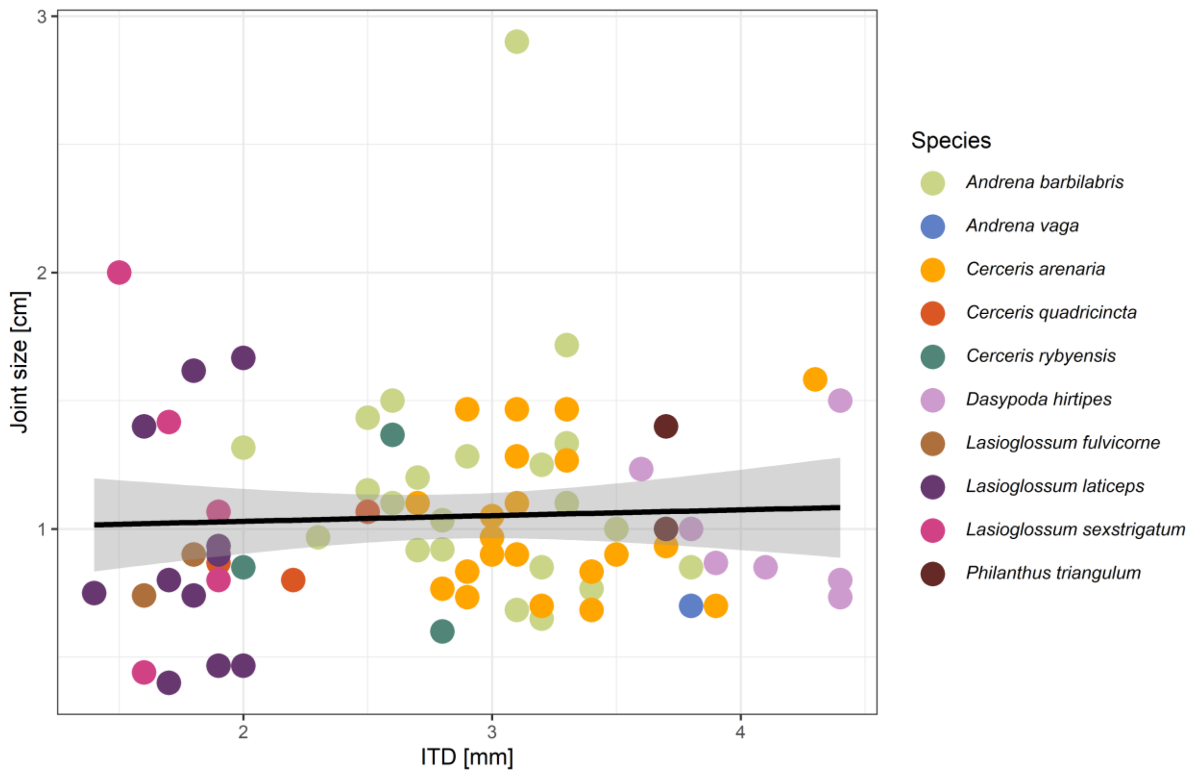

Fig. 4 Linear regression of inter-tegular distance average (ITD in mm) and joint size average (in cm). Colors corresponded to different ground-nesting species. Grey shade area indicates 95% confidence interval region computed from means.

Joint structure and pavement type

After excluding 10 sites because they did not meet our classification (i.e. hybrid pavement, ..), a total of 79 sites were characterized. The joints were mostly unbound, accounting for 80% of the sites encountered, while 20% of the joints were characterized as rigid and degraded, leaving openings for ground-nesting species to dig and nest (Fig. 5a). In terms of composition, the pavements were mainly composed of concrete slabs (40 sites) and sandstone setts (29 sites) (Fig. 5b). The remaining sites were composed of sandstone or limestone paving stones (3 sites), concrete paving blocs (4 sites), ceramic paving flags (1 site), porphyry setts (1 site) and blue stone elements (1 site). Regarding to the location of nests on the pavements (Fig. 5c), most were located on sidewalks (53 sites) while some were located on roads (3 sites) and in the internal courtyards of houses (8 sites). Some sites were located only at the level of house steps (11 sites) or sometimes spilling over onto sidewalks (2 sites). Only one site was characterized on stair steps and another one was characterized with an overflow of the ground-nesting aggregation from the embankment to the sidewalk.

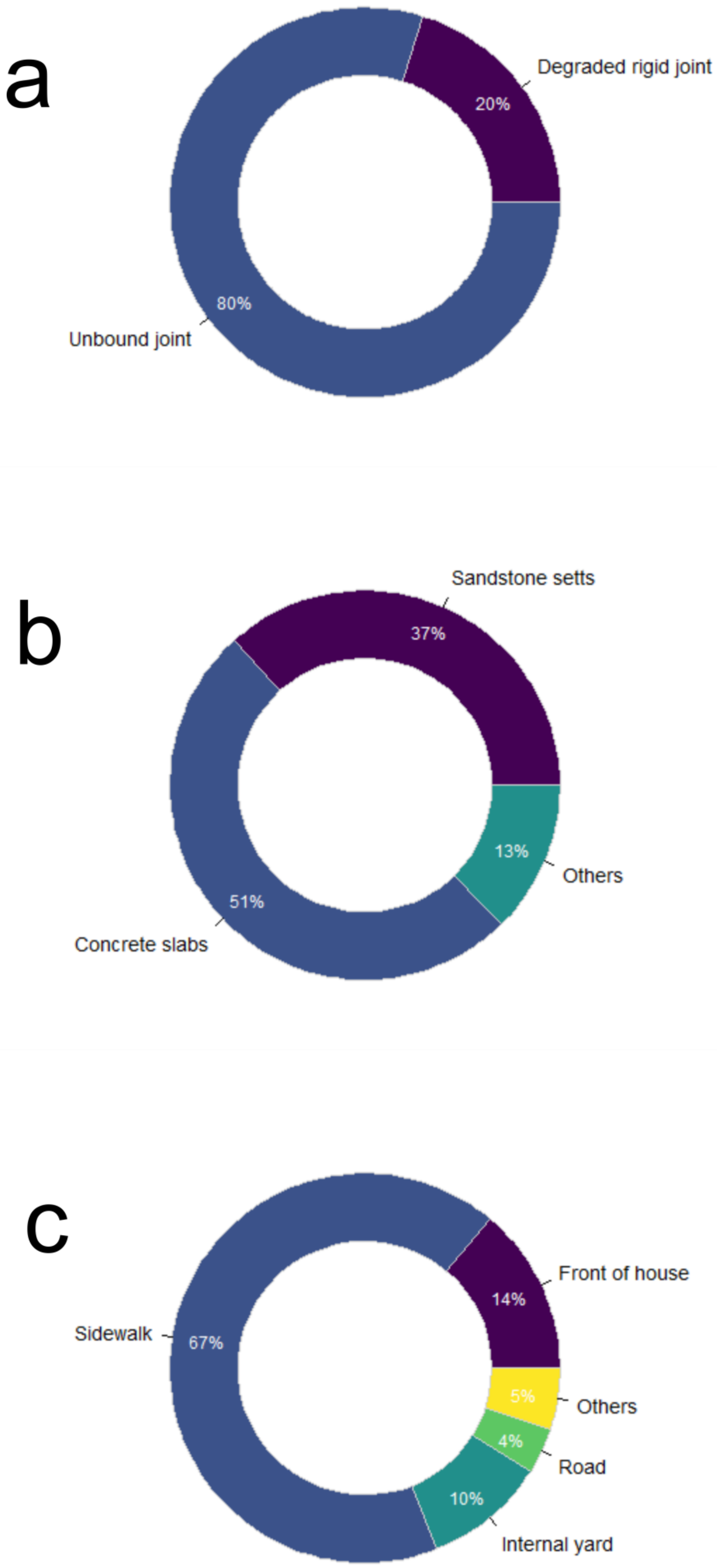
a
Degraded rigid joint
20%
80%
Unbound joint
b
Sandstone setts
37%
13%
Others
51%
Concrete slabs
c
Front of house
14%
Sidewalk
67%
5%
Others
4%
Road
10%
Internal yard

Fig. 5 Distribution (%) from 79 study sites of joint types (**a**), kinds of urban pavement on which nests were located (**b**) and nest locations on urban pavements by site (**c**).

Soil texture analysis

A total of 53 sandy mound samples were analysed for grain size. The particle size analysis method did not allow us to distinguish between clay and silt composition. The sandy fraction of the samples was always higher than 85% and the silt and clay fractions were always lower than 10%, classifying all samples as sandy and homogeneous in texture (Fig. S3). On average, the samples were composed of 2.91% of particles larger than 1mm in diameter (i.e., very coarse sands) and 2.61% smaller than 50 µm (i.e., clays and silts). Particles with a diameter of 500 µm - 200 µm (i.e., medium sands) were the most abundant in the samples with a proportion of 41.71%. The samples contained on average 7.47% of particles in the 1 mm – 500 µm class (i.e., coarse sands), 13.40% of particles with a diameter of 100 µm – 50 µm (i.e., very fine sands) and 31.90% of 200 µm – 100 µm (i.e., fine sands) (Fig. S4). PCA did not detect distinguished clusters or discontinuities of the sandy samples according to the ground-nesting species or their respective families (Fig. 6).

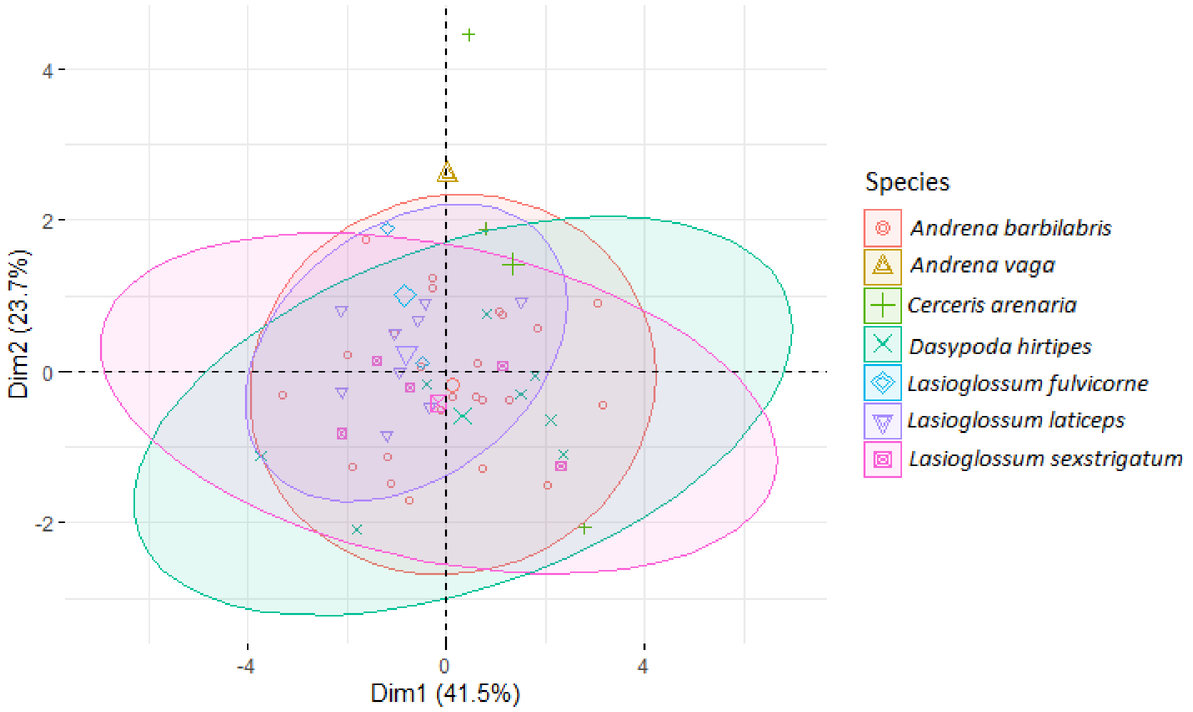

Fig. 6 Principal component analysis (PCA) of collected tumuli samples grouping with 80% confidence ellipses by ground-nesting species. Dimensions 1 and 2 showed 65.2% of the explained variance. Coloured and shaped points (N = 53) corresponded to the ground-nesting species.

Discussion

Monitored species

At present, knowledge about adaptations of these ground-nesting bees to the urban environments is patchy, particularly with regards to their nesting strategies (Wenzel et al. 2020b; Antoine and Forrest 2021; Ayers and Rehan 2021). In our study, we were able to confirm the observations of Pauly (2019a) and Haeseler (1982) for *D. hirtipes*, *L. laticeps* and *A. barbilabris* (the latter also having been mentioned by Falk (2015)), but not for the Halictidae bee species *Lasioglossum calceatum* (Scopoli, 1763), *Halictus rubicundus* (Christ, 1791) and, *Sphecodes puncticeps* Thomson, 1870 and, for the Andrenidae bee species *Panurgus calcaratus* (Scopoli 1763). We may have missed the presence of this oligolectic specimen of *Heriacium* spp. (Asteraceae) due to its summer phenology (Rasmont and Haubruge 2002). However, some species of ground-nesting bees or their associated cleptoparasites were identified for the first-time nesting under the urban pavements: *A. vaga*, *L. fulvicorne*, *S. crassus*, *S. monilicornis* and, *N. alboguttata*. These 11 species of ground-nesting bees and cuckoo bees rather common, and are not concerned by an extinction status in Belgium and Europe with stable populations, except for *A. barbilabris* whose Belgian populations are reported to be increasing (Nieto et al. 2014; Drossart et al. 2019). All wild bees are polylectic except for *A. vaga* and *D. hirtipes* which are specialists for *Salix* spp. (Salicaceae) and some genera of Asteraceae, respectively (Rasmont and Haubruge 2002). Compared to the co-occurrence data with their associated hosts (Fig. S2), it appears that *L. laticeps* may be a new host for the cuckoo *S. crassus,* although we cannot confirm the association by an observed entry into the nest. We also captured a specimen of *S. monilicornis* which would be a potential cuckoo bee of *L. laticeps* (Bogusch 2003). We can confirm Vegter's (1993) observations of large numbers of *S. miniatus* parasitizing *L. sexstrigatum* nests. Finally, three specimens of *S. pellucidus* and five of *N. alboguttata* were captured at sites of its known host *A. barbilabris* (Witt 1992; Rasmont and Haubruge 2002).

In the scientific literature, only one mention of 9 apoid ground-nesting wasps and 1 spider wasp species (Hymenoptera: Pompilidae) in urban pavements of the city of Oldenburg (Germany) has been reported by Haeseler (1982). Our document is therefore the second written mention of apoid wasps nesting under urban pavements with 8 new species (only *O. bipunctatus* is present in both studies). As in Haeseler (1982), the species richness of apoid wasps in BCR is greater than that of the identified ground-nesting bees. The three *Cerceris* species are solitary wasps that nest on sandy substrates. They capture and paralyse small Coleoptera for their offspring, especially Curculionidae or Chrysomelidae specimens for *C. arenaria* and *C. quadricincta* while *C. rybyiensis* specialises in capturing small species of halictid bees (Bitsch et al. 1997). *H. gerstaekeri* and *H. nobile* are known as their nest parasitoid wasps. *P. triangulum*, commonly known as the "beewolf", is a predatory apoid species that is widespread in Europe. It is a specialist predator of *Apis mellifera* L., but can exceptionally substitute for other wild bee genera (e.g. *Andrena* spp., *Dasypoda* spp.) (Bitsch et al. 1997).

Surprisingly, other species of apoid wasps belonging to other genera, smaller and less frequently captured, were also found among the pavement inhabitants. These were *G. planifrons*, *D. insidiosus*, *M. lutaria*, *O. bipunctatus* and *L. pygmaeus armatus*. Their nests often consist of a single gallery leading to the larval cell(s) in sandy soils. Like *Cerceris* spp., the adults are generalist predators. Their prey consists mainly of specimens belonging to the families Cicadellidae, Fulgoridae, Cercopidae, Membracidae, micro-Diptera or micro-Hymenoptera (Bitsch and Leclercq 1993; Bitsch et al. 1997, 2007). These small apoid wasps are common species in Belgium (Bitsch et al. 1997) and have no conservation status in Belgium, although *G. planifrons* is considered as very rare (Schmid-Egger et al. 2010). However, *L. pygmaeus armatus* is a rare psammophilous species in Belgium, with only two observations since 1950 despite its wide European range (Bitsch and Leclercq 1993; Rasmont and Haubruge 2002). This species was observed on 4 different sites in BRC, suggesting that it nests frequently on BRC pavements and could therefore be the subject of a conservation project. Another interesting finding of our study was that the nest aggregation was mixed with species such as *C. arenaria* and *D. hirtipes* in many sites (Fig. S2). From our sampling protocol, it was difficult to observe nest differentiation or sharing between ground-nesting species. Furthermore, intraspecific individuals of *Cerceris* species can co-occupy the same nest (Willmer 1985; Polidori et al. 2006), which calls into question their strictly solitary behaviour. Therefore, it would be interesting to excavate the nest and observe whether both species groups share their larval cell structure.

Our sampling was limited to a single sampling period of 30 - 45 minutes. It is likely that the entire diversity per site was not sampled. It should be noted that nest-aggregations are dynamic systems and the counts taken only reflect a moment in time in the life of ground-nesting insect populations and communities. From a spatial point of view, this study was limited to the Belgian capital with its own urbanization and climatic conditions. Therefore, an extension of this study to other large cities (e.g., Paris or Berlin) could highlight other species of ground-nesting bees and wasps in urban pavements and which may have different conservation issues. Finally, nests in crowded streets with large nest aggregations and large identified species such as *Andrena* spp., *D. hirtipes*, *P. triangulum* or even *Cerceris* spp. were more prone to be detected. On the other hand, small species nesting within the pavements such as *Lasioglossum* spp. or the other small-sized apoid species (Table 1) may have been undetected because they were located in less frequented streets, and characterized by small nest clusters with poorly visible sand mounds. We can therefore assume that our sampling effort may have overestimated the number of large species and underestimated small species.

Joint size and pavement structure

Joint sizes in BCR vary from 1mm to 1.5cm depending on the shape of the pavement element and the maximum diameter of the jointing material (Bruxelles-Mobilité 2016). However, during our observations, we found that the size of the jointing material at the entrance to the galleries fluctuated around a wider average, with no real distinction between species or families of apoids. An increase in distance between two tiles or slabs is likely to lead to degradation of the pavement. Otherwise, we did not observe any preference for joint size according to the taxonomy or the species size suggesting that the measured ITD was generally sufficient to allow a wide range of species to pass through the narrowest joint measured.

All sites showed openings in the joints between the pavement tiles, which allowed the ground-nesting species to dig their galleries. Nest entrances could be observed if (1) jointing material was absent, (2) jointing material was unbound or (3) bound jointing material was degraded. The presence of galleries in cracks of bonded joints highlighted in the results was rather surprising. These structures were designed to be completely closed and did not allow insects to nest. At the same time, however, we observed deterioration of the pavement and fragmentation of the jointing material. This could be explained by the poor quality of the rigid joint or its age, which affected the durability and cohesion of the material, making it more prone to disintegration during any disturbance such as shrinkage cracking or freeze/thaw episodes. Alternatively, ground-nesting species of bees and wasps could be involved in the degradation of the modular structures and in particular their joints, as bees are able to dig into hard-packed soils (Barthell et al. 1988; Cane 1991).

A BCR pavement with unbound jointing materials is theoretically always coupled with underlying permeable and draining layers (i.e., sand, gravel, stone) in order to avoid water stagnation in the structure and its deterioration (CRR 2009, 2018). This combination seems to correspond to the criteria of sandy texture and drainage of the soil material generally required by ground-nesting bees and wasps in their natural environment. Indeed, a soil that is too waterlogged, flooded or too dry can jeopardise the survival capacity of individuals in immature stages (Wuellner 1999). Most of the pavements consisted of sandstone blocks and concrete slabs. This suggests that pavement thickness and type may have little effect on nesting site preference for any ground-nesting species. These results raised many questions about the possible multiplicity of gallery forms within the substrate. Although we were able to determine the depth at which we found individuals of *A. barbilabris* (see supplementary information

1), the architecture of the sub-pavement nests remains unknown: do the galleries penetrate deep into the different layers that make up the paving, or do they extend to the first few centimetres below the paving? In addition, we can wonder whether the choice of nest site was due to a preference for concrete slabs and sandstone pavement, or whether their location was simply the result of the greater availability of these types of paving in the BCR.

As for the results relating to the location of the sites on the pavement, they enable us to highlight phenomena that had not been recorded to our knowledge in the literature until now. Indeed, although our observations suggested that many individuals nested on pavements only, we also observed nesting sites at the level of house steps and stairways. This observation was accompanied by a lack of jointing material along these terraced houses, which allowed easier access to the sandy stratum under the pavements for ground-nesting species. It was mainly *Lasioglossum* spp. and non-Philantidae wasp species that preferred to nest in this type of location, which also should allow them to benefit from higher temperatures due to indirect solar radiation (Cane 2015) that first reaches the facades of the terraced houses.

Soil texture analysis

The particle size analysis revealed that the mound samples corresponded to the sandy texture. This texture classification was consistent with observations made by Cane (1991) on 32 species of ground-nesting bees in the USA, by Vereecken *et al.*, (2006) for *A. vaga*, Malyshev (1935) and Michez (2007) for *D. hirtipes*, and Falk (2015) for the 6 remaining bee species, which determined that these ground-nesting bees built their nests on sandy-textured soils. However, while these authors noted a variety of other used textures, such as silt loam and clay loam for Cane (1991), sandy-clay soils also for Vereecken *et al.*, (2006) or clay soils also for Michez (2007), our study highlighted only one type of texture used by the bees to dig their galleries. This means that the foundation layer could be homogeneous in all BRC pavements if it was of sandy origin. On the other hand, promoting a sandy and homogeneous texture through urban redevelopment would disproportionately favour specific populations associated with this effective ecological niche.

Implications for urban pavement design and their management

A suitable pavement for ground-nesting species consists of sandstone pavers or concrete slabs with an unbound jointing size around 1cm on an unbound foundation. However, this pavement hosting ground-nesting species was only an archetype (Fig. 7) from the results of our study. It seems difficult to modify the requirements of the standard specifications established by the BCR specifications, as these are the basic rules to guarantee the durability of the pavement (Bruxelles-Mobilité 2016). While natural stone pavements with wide and unbound joint were more favourable as nesting sites for the studied apoid species, these generally offer a lower level of pedestrian comfort (Bertrand et al. 2019) and are not fully compatible with the durability requirements of the BCR specifications which recommend modular structures of the bonded type and with joint openings less than or equal to 1 cm (Bruxelles-Mobilité 2016).

This finding highlights a mismatch between the societal demands of BCR and the environmental opportunities. We therefore propose new pilot studies to assess the possibility of designing multifunctional pavements that could simultaneously meet the challenges of comfort, durability, entomobiodiversity and rainwater infiltration. Either through technological advances in paving block design, or by differentiating pavements with a central area dedicated to pedestrians (no or thin joints) and a peripheral area dedicated to the reception of ground-nesting species and water infiltration (wide joint openings, draining material, vegetated or not), or by creating and/or maintaining a vegetated strip at the periphery of pavements, as may exist in BCR allotments (Fig. S5). It would also be interesting to foster actions to initiate and reinforce a paradigm shift in the city's aesthetic criteria: "untidy" and "unfunctional" pavements in the human-centred city could become "multifunctional" pavements in the bio-centred city (Aronson et al. 2017; Rivkin et al. 2019). It would be very interesting to link this multifunctionality not only to biodiversity (i.e., offering nesting opportunities for ground-dwelling wild bees and other insects), but also with a potential for water leaching and an urgently needed reduction of soil sealing in urban areas (Fini et al. 2017)..

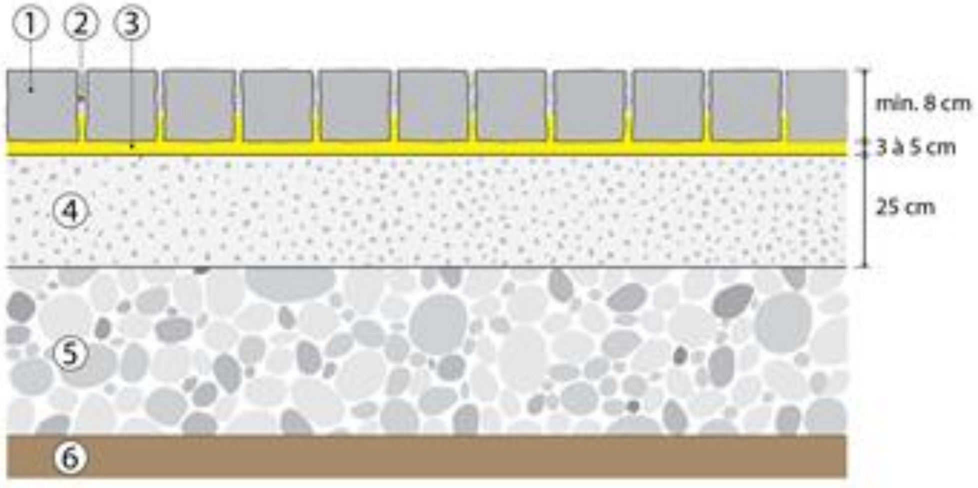

Fig. 7 The pavement structure : (**1**) Paving elements ; (**2**) Joints with an opening size of 0.8 to 1.0cm, filled with sand 0/6.3 or 0/8 (fine content less or equal than 10%); (**3**) Laying course: gravel 2/6,3 or 2/8 (fine content less or

equal than 2%); (**4**) Road base: unbound aggregate 0/20 or 0/40; (**5**) Sub-base with defined thickness according to the construction plan; (**6**) Subgrade

Conclusions

Our results show that sealed surfaces in urban areas do not always lead to the total loss of nesting opportunities as suggested by Cane et al., (2006) and Fortel et al., (2016). On the contrary, our study highlighted the opportunity of these structures in terms of nesting resources in the city. Our observations tend to confirm the hypothesis put forward by Pauly (2019a), who stated that among all the pavement types in BRC, the old pavements in BCR - where the soil under the paving stones was sandy and where the joints were not cemented - were the most hospitable for ground-nesting bees and consequently for ground-nesting wasps. Unfortunately, these older BCR pavements are more prone to be redeveloped into pavement that is less suitable as nesting sites by the city of Brussels. This study suggests that pavements, previously thought to be unsuitable for biodiversity, may provide a refuge for some insect populations. Therefore, by modulating pavement design and proposing alternative construction models, we could make the city a more welcoming place for biodiversity.

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Statements & Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose

Author Contributions

All authors contributed to the study conception and study design. Material preparation and data collection were performed by Grégoire Noël, Violette Van Keymeulen, Sylvie Smets and Olivier Van Damme. Analysis was performed by Grégoire Noël and Violette Van Keymeulen. The first draft of the manuscript was written by Grégoire Noël and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability

The R code and the data used in this paper are available at https://github.com/gregnoel/Street_Apoid.git